

A TAXONOMIC RE-INTERPRETATION OF THE OROBANCHE CALIFORNICA COMPLEX

LAWRENCE R. HECKARD

Jepson Herbarium, University of California, Berkeley 94720

Considerable difficulty has been encountered in classifying plants treated by Beck (1930) and Munz (1930) as *Orobanche californica* and *O. grayana*. Sporadic inconstancies in nearly all morphological characters result in puzzling variation patterns and combinations of features that form groups that are not readily defined taxonomically. This complexity has led me to make a taxonomic re-evaluation of these groups. Moreover, a study of collections made since 1930, as well as of type specimens available to me but not seen by either Beck or Munz, suggests changes in both the taxonomy and nomenclature of these plants.

The plants treated here belong to **Orobanche** L. sect. **Nothaphyllon** (A. Gray) Heckard, comb. nov. [Basionym: *Aphyllon* Mitchell sect. *Nothaphyllon* A. Gray, Bot. Calif. 1:584. 1876. Lectotype species here designated: *Aphyllon californicum* (C. & S.) A. Gray = *Orobanche californica* C. & S.]. This section, a small but widespread group of American species, was previously called *Orobanche* L. sect. *Myzorrhiza* (Phil.) Beck (Bibl. Bot. 4:78. 1890) on the erroneous assumption that the genus *Myzorrhiza* Philippi (Linnaea 29:36. 1858) established priority for the sectional name.

In my judgment the plants treated as two species, *Orobanche californica* and *O. grayana*, by Munz and by Beck comprise four species. The relative distinctness of one of these four, *O. corymbosa* (Rydberg) Ferris of the Great Basin, was pointed out by Ferris (1958) when she gave specific rank to *O. californica* var. *corymbosa* (Rydb.) Munz. This species is not treated further in this paper except in the key to species. My recognition of a second species, *O. parishii* of southern California and environs, is reflected in the raising of *O. californica* var. *parishii* Jepson to specific rank. I propose two subspecific taxa to encompass its geographic variants. Treatment of the remaining two species involves nomenclatural changes owing to a reinterpretation of the type specimens as well as to changes in taxonomic circumscription. One of these species is a widespread and morphologically complex species with six subspecies in the western United States and contiguous areas, and the other is a monotypic species confined to California. The widespread, variable species has heretofore been called *O. grayana* but should properly be named *O. californica*. The other species previously called *O. californica* must have a new name and I have selected *O. vallicola*.

My revision has been based on herbarium specimens and living specimens, when available. *Orobanche* is often difficult to find in the field, although searching at localities listed on herbarium labels was in some instances successful. The plants are becoming increasingly scarce with the spread of man's activities. In order to document the occurrence of these rare plants I am citing one specimen from each of the known localities.

Chromosome counts in this group (Chuang & Heckard, in prep.) are mostly $n = 24$, but $n = 48$ has appeared in two species, *O. corymbosa* and *O. parishii*, indicating that polyploidy may be one of the causes of taxonomic difficulties.

Thieret (1971) pointed out that the biology of most Orobanchaceae is poorly known and even such basic information as the hosts for these parasitic plants is seldom noted by collectors. From the host data assembled in this study there appears to be some host specificity for the species recognized here. Indeed, this difference is one of the reasons for retaining *O. californica* and *O. vallicola* as distinct species. While *O. vallicola* is frequently reported growing on the roots of trees and shrubs, *O. californica* is chiefly reported on herbaceous perennials, largely of the Compositae. Occasional reports of *O. californica* on various plants other than those of the Compositae need confirmation. There is some evidence of host specificity at the subspecies level within *O. californica* as is indicated under each subspecies.

TAXONOMIC CHARACTERS

Formulating a taxonomy for the species of this complex is hindered by the limited number of morphological features available for comparative purposes and by the sporadic inconstancy of most of these features.

The characters used in this study, except for overall sizes, are all in the inflorescence or flower. Significant differences in plant size do exist and involve independent variation in length of stem and inflorescence. Vertical measurements are given in this paper in terms of length rather than height in order to avoid any confusion with the above-ground height. The entire stem and often the lower portion of the inflorescence remain below ground.

Associated with plant size are differences in inflorescences (figs. 1, 2) that are of diagnostic value. These differences are only of degree and are modifications of a general branched (paniculate) inflorescence (fig. 1, M). Failure of the branches to develop on the main axis results in a simple racemose or spicate inflorescence (fig. 1, N) and this may occur within the same population or even in the same plant on a second stem arising from the base of a cluster. Whether the simple inflorescences are racemose or spicate is problematical since the flowers are usually sessile (at the top) and pedicelled (at the bottom) in the same inflorescence. Occasionally either the sessile or pedicelled condition is present exclusively in an inflorescence. This is especially true for *O. vallicola*, in which both conditions as well as the mixed one are present. The term subspicate has been used in this paper to describe the inflorescence that

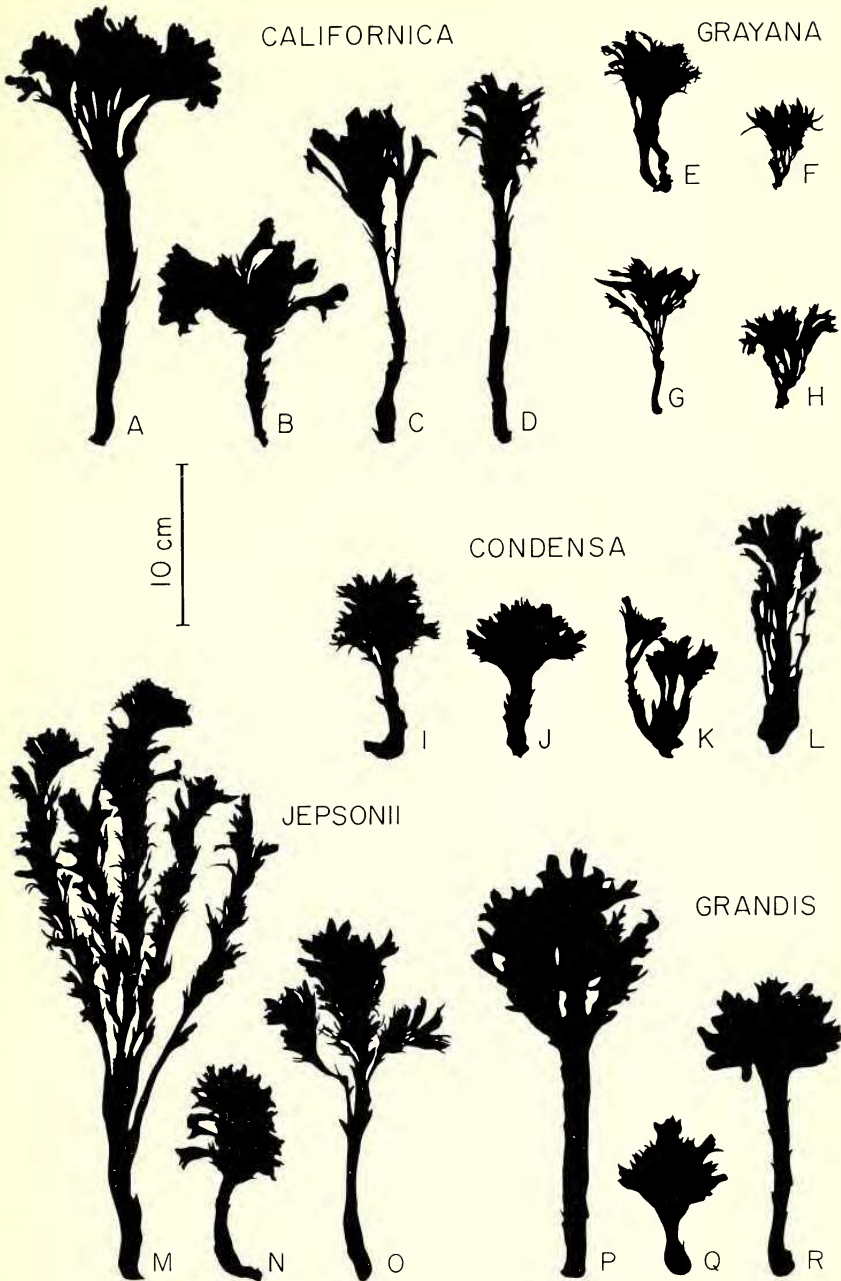


FIG. 1. Silhouettes of herbarium specimens of *Orobancha californica* showing habit and size. A-D, ssp. *californica*. A, Roderick in 1961; B, Setchell in 1909; C, Setchell in 1908; D, Otis 2350. E-H, ssp. *grayana*. E, F, Suksdorf in 1882; G, Nutting in 1915; H, Beans in 1914. I-L, ssp. *condensa*. I, Lee 1055; J, Bacigalupi 5242; K, Condit in 1910; L, Bacigalupi 5128. M-O, ssp. *jepsonii*. M, Chandler in 1905; N, S. G. Smith 2658; O, Brewer 1273. P-R, ssp. *grandis*. P, Wood in 1946; Q, Hoffmann in 1930; R, Pollard in 1954.

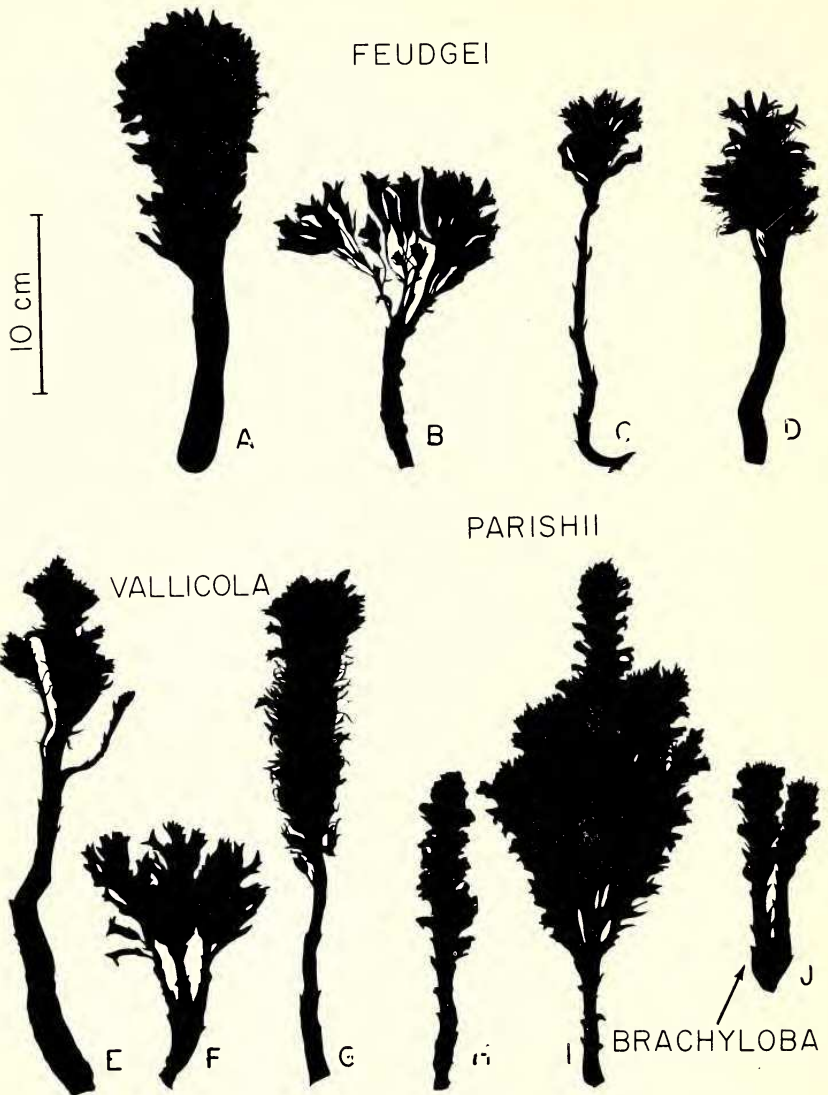


FIG. 2. Silhouettes of herbarium specimens of the *Orobanche californica* group showing habit and size. A–D, *O. californica* ssp. *feudgei*. A, *Breedlove* 4010; B, *Hall* 6327; C, *Munz* 5827; D, *Abrams & McGregor* 654. E–G, *O. vallicola*. E, *Barber* in 1898; F, *Murphey* in 1946; G, *Jepson* 6196 (holotype). H–I, *O. parishii* ssp. *parishii*. H, *T. Brandegee* in 1894; I, *Davidson* in 1889. J, *O. parishii* ssp. *brachyloba*, *Raven & Thompson* 20794 (holotype).

has both sessile and pedicelled flowers. This inflorescence is characteristic of both *O. vallicola* (fig. 2, G) and *O. parishii* (fig. 2, H). The inflorescence of both these species (fig. 2, E, F, I) may also be branched

and thus "paniculate", as is that of *O. californica* ssp. *jepsonii* (fig. 1, M, O), but the latter often has the branches racemose rather than subspicate. Another variation in the inflorescence involves a greater elongation of the pedicels of the lowermost flowers along with a shortened inflorescence and results in the subcorymbose inflorescence characteristic of *O. californica* ssp. *grayana* (fig. 1, E-H). This inflorescence is present along with subspicate ones in ssp. *californica* (fig. 1, A-C), ssp. *feudgei* (fig. 2, B), and ssp. *grandis* (fig. 1, Q-R). When the paniculate or racemose inflorescence is both reduced and congested, it is described as subcapitate, as in ssp. *condensa* (fig. 1, I, K).

Bract shape and the number of parallel veins of the bract are useful features for distinguishing *O. parishii* from *O. vallicola*. The bracts of *O. parishii* (fig. 3, L-N) are ovate to lance-ovate and have seven or more conspicuous parallel veins, while those of *O. vallicola* (fig. 3, I-K) are lanceolate and have about five or less veins. In herbarium material, the bracts of *O. parishii* are lighter in color and the veins are much more conspicuous, which may indicate a thinner bract. The bract of *O. californica* (fig. 3, H) is usually broader than that of *O. vallicola* but similar in venation pattern.

Flower characters (fig. 3, A-G) useful in taxonomy are: color; size of parts, especially length of corolla and lips; shape of corolla lobes, especially whether the apex is rounded or pointed; degree of spreading of corolla lips; and shape of stigma. The stigma varies in thickness, in degree of development of the bilobed condition, and in degree of outward curvature of the apex and margins of the lobes. Spreading lobes that are not rolled outward at the margins (infundibular) characterize *O. californica* (fig. 4, D, F), although sporadic variants (fig. 4, A, B) in ssp. *californica* have the margins rolled downward (crateriform). The strongly bilobed stigma with conspicuously curved lobes is diagnostic for *O. vallicola* (fig. 4, J-L). The stigma of *O. parishii* (fig. 4, G-I) is somewhat infundibular or occasionally has curved margins.

REINTERPRETATION OF THE TYPE OF OROBANCHE CALIFORNICA

The type specimen of *Orobanche californica* Chamisso & Schlechtendal is a single, reduced, and fragmentary plant collected in October 1816 in the vicinity of San Francisco. The type is more similar to coastal bluff plants than to inland plants in the following features: 1) the corolla of the type is dark reddish-brown while in inland plants it is much lighter; 2) the corolla is tougher, thicker, and less brittle in the type than in inland plants; 3) the dimensions of the corolla (23 mm long with lips up to 10 mm long) are within the lower part of the range of coastal bluff plants but slightly exceed the usual lip length of inland plants, and the upper lip and lobes are broader than in inland plants; 4) the anthers are moderately heavily villous, an exceptional condition in inland plants. Therefore, I disagree with the current practice of applying the name *O. californica* to inland plants, for which I propose the name *O. vallicola*.

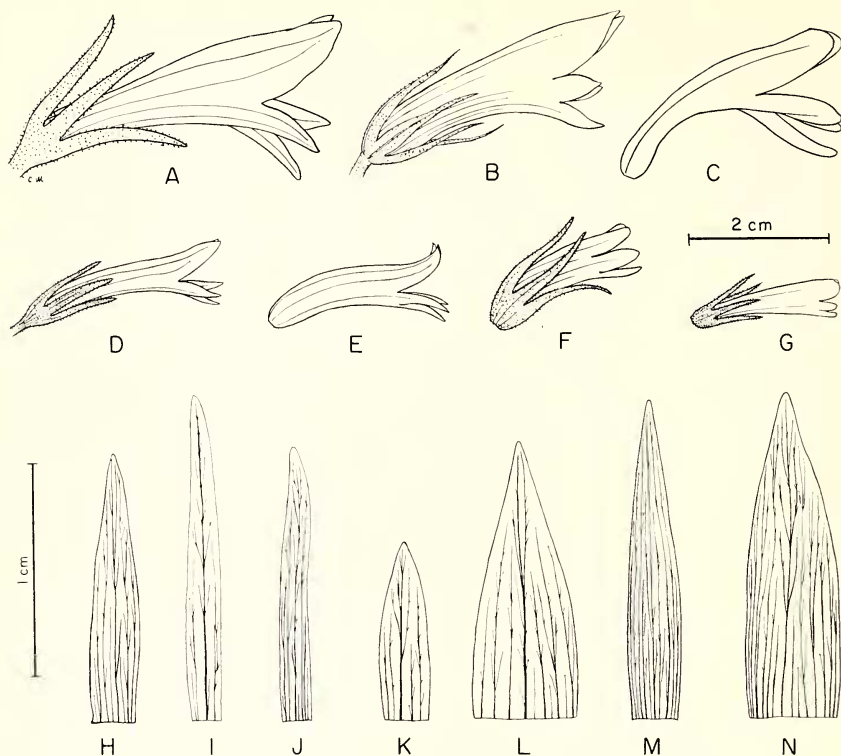


FIG. 3. Flowers (A-G) and bracts (H-N) in the *Orobanchae californica* group: A-G, *O. californica*. A, ssp. *grandis* (Pollard, holotype); B, ssp. *feudgei* (Munz 5827); C, ssp. *californica* (Roderick in 1961). D-E, *O. vallicola* (D, Kessell, 16 Sep 1956; E, Lile, 1 Oct 1933). F-G, *O. parishii*, F, ssp. *parishii* (Pierson 416); G, ssp. *brachyloba* (Raven & Thompson 20794). H, *O. californica* ssp. *jepsonii* (Chandler, holotype). I-K, *O. vallicola* (I, Crawford 547; J, Jepson, holotype; K, Murphey, 16 Oct 1946). L-N, *O. parishii*. L-M, ssp. *parishii* (L, Clokey 5308; M, Gander 286); N, ssp. *brachyloba* (Raven & Thompson 20794).

Orobanchae californica should instead be applied to coastal bluff plants, which heretofore have been called *O. grayana* var. *violacea* (Eastw.) Munz.

Munz (1930) was probably misled in his interpretation of *O. californica* by Chamisso and Schlechtendal's erroneous description of the anthers as sparingly or moderately villous. Actually the anthers of the type are quite villous with the hairs concentrated mostly along the dehiscence suture but also present on the back of the anther. Certainly the anther indument is well within the range of that in coastal bluff plants, but it would be an extreme condition or exception for *O. vallicola*.

The one feature of the type specimen that is more typical of *O. vallicola* than of coastal-bluff plants is the crateriform stigma with revolute

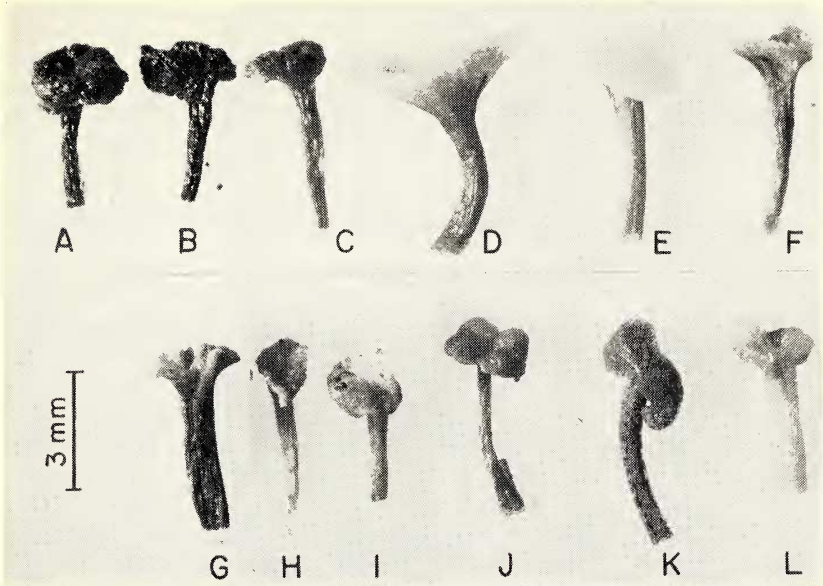


FIG. 4. Stigma types in the *Orobanche californica* group. A-C, *O. californica* ssp. *californica*. A, Eastwood in 1900 (isotype of *Aphyllon violaceum*); B, Chamisso & Eschscholtz, Oct 1816 (holotype of *O. californica*); C, Crampton 5915; D, *O. californica* ssp. *feudgei*, Holmgren & Reveal 2598; E, *O. californica* ssp. *grandis* (Norris in 1968); F, *O. californica* ssp. *jepsonii*, Chandler (isotype of *O. grayana* var. *jepsonii*). G-I, *O. parishii* ssp. *parishii*; G, Davidson, Aug 1899; H, Johnston 1762; I, Alderson 8327. J-L, *O. vallicola*. J, Jepson 6169 (isotype of *O. comosa* var. *vallicola*); K, Kessel in 1966; L, Crawford 547 (isotype of *O. californica* var. *claremontensis*).

margins (as in fig. 4, J-K). Stigma shape, however, is variable in both species and this stigma type is occasionally encountered in the coastal bluff form (fig. 4, A, C).

Attempts to re-collect an *Orobanche* similar to the Chamisso plant in San Francisco have not been successful. There is no apparent reason why plants similar to the Chamisso collection should not be found in suitable habitats around the ocean bluffs of San Francisco. Similar plants grow on coastal bluffs within 25 km to the south and 50 km to the north. On the other hand, the nearest collection of *O. vallicola* is in Marin Co. about 30 km north of San Francisco and in a less maritime environment.

TAXONOMY AND DISTRIBUTION

It is important to preface a taxonomic treatment and identification keys for this group of *Orobanche* with a word of caution concerning the perplexing variability in the group. There is an inconstancy in the inflorescence and floral characters that are used in formulating a taxonomy for these plants. Natural units, morphologically, ecologically, and geo-

graphically defined, do exist, but sporadic inconstancies may occur within these units in an entire population or portion of one. These variations result in overlap of the diagnostic characters separating the taxa and cause difficulty in formulating keys that will identify all the variant plants of a taxon. The keys of this treatment are constructed to account for some of this variation but not all, and plants exceptional in any one feature may be encountered.

The relationship of the considerable variability of these *Orobanche* to their parasitic habit is problematical. Ernst (1972) suggested in the case of hemiparasitic plants that parasitism may expand opportunities for survival and sympatric occurrences. Extension of the life expectancy of plants with reduced or marginal fitness could enrich their genetic and morphological diversity. Ernst's conclusion that taxonomists might be well advised to accept broader patterns of variation in superficial morphology for hemiparasitic plants should be valid also for holoparasites.

KEY TO THE SPECIES OF THE *OROBANCHE CALIFORNICA* COMPLEX

- Corolla 2.5–5.0 cm long; corolla lips 10–14 mm long, widely spreading;
British Columbia to N Baja California, mostly in or W of the Cascade-Sierra-Peninsular ranges 1. *O. californica*
- Corolla 1.5–2.5 cm long; corolla lips 4–10 mm long, erect to spreading.
Inflorescence spicate; upper corolla and lips white, yellow, pinkish, or buff, often with deep reddish or purplish veins; anthers glabrous or villous mostly along the dehisced margins; California and Baja California.
- Corolla lobes acute with mostly pointed apices; cauline bracts lanceolate with 5 or fewer inconspicuous parallel veins, dark brown in dried specimens; cismontane California from Trinity Co. S to Los Angeles Co. 2. *O. vallicola*
- Corolla lobes obtuse with rounded to blunt apices; bracts ovate to lance-ovate with more than 5 conspicuous parallel veins, light brown or buff in dried specimens; Southern California and Baja California 3. *O. parishii*
- Inflorescence corymbose or subcorymbose (becoming spicate in the Columbia Plateau); upper corolla and lips purplish on inner surface, paler and grayish on exterior; anther surface densely villous; sagebrush areas, Great Basin and Columbia Plateau and environs *O. corymbosa* (not treated)

1. *OROBANCHE CALIFORNICA* Chamisso & Schlechtendal, *Linnaea* 3:134. 1828. *Phelipaea californica* (C. & S.) G. Don, *Gen. Hist. Plants* 4:632. 1838. *Aphyllon californicum* (C. & S.) Gray, *Bot. Calif.* 1:584. 1876. *Myzorrhiza californica* (C. & S.) Rybd., *Bull. Torrey Bot. Club* 36:695. 1909. TYPE: “. . . e vicinia portus St. Francisci Californiae . . .”, *Chamisso & Echscholtz.* (HOLOTYPE: LE!; Photograph, JEPS).

Plants 4–35 cm in length, only the inflorescence above ground, the

subterranean stem portion 1–15 cm long; stems solitary to fastigiate branched, slender to stout (5–20 mm in diameter), bearing broadly ovate to subulate scales mostly less than 10 mm long; host attachment consisting of a few coralloid strands, only rarely forming an irregular bulbous mass; inflorescence subcorymbose or subspicate to racemose, glandular-puberulent throughout; pedicels mostly well-defined below, decreasing in length upwards in the inflorescence from 1–4 cm above to 0–1 cm in length, bearing 2 opposite or variously placed linear-subulate bractlets 5–10 mm long; calyx with subulate to linear-subulate, gradually attenuate lobes, 6–20 mm long; corolla strongly bilabiate, 22–45 mm long, white to pale rose and deep purple with yellow palatal folds, sparsely to moderately glandular-puberulent externally; corolla lips mostly widely spreading, 8–15 mm long, the upper lip usually slightly longer than the lower lip; lobes of upper lip deltoid to broadly deltoid with bluntly acute or rounded apices; lower lip parted into 3 lanceolate lobes; corolla tube arching forward placing the throat in a horizontal position; anthers densely villous, especially along the dehiscence suture, rarely glabrous; stigma variable in size, mostly with triangular, widely spreading to revolute lobes; capsule ovoid to cylindrical-ovoid, 10–12 mm long; seed cuneiform, favose-reticulate, 0.4–0.6 mm long.

HOSTS: Various perennials, chiefly of the Compositae (see each subspecies for specific hosts).

DISTRIBUTION: In and west of the Cascade-Sierra Nevada-Peninsular ranges from Vancouver Island, British Columbia, S to the Sierra San Pedro Martir in Baja California (fig. 5). Elevation 0–2,400 m.

Formulating an infraspecific classification of *O. californica* is impeded by the considerable variability in the rather few morphological features that must be relied upon for taxonomic delimitation and by sometimes baffling disjunction in the distribution of the variants. There is clearly a series of geographic variants that deserves taxonomic recognition, however, and this treatment attempts to point out the most significant of these by according them subspecific status. Subspecific delineation is based on features of habit (fig. 1, 2); corolla color, size, and shape (fig. 3); and to a lesser degree host preference. Anomalies in morphology or distribution and attendant problems in creating a workable classification are discussed with the appropriate subspecies.

KEY TO SUBSPECIES OF OROBANCHE CALIFORNICA

- Upper corolla tube and lips dark violet; calyx lobes, pedicels, and bracts violet-tinged, drying blackish purple; coastal dunes and hills from the Monterey Peninsula, California, N to southwestern British Columbia. la. ssp. *californica*
- Upper corolla tube and lips white or yellowish to pinkish or purple-tinged, often with the veins pink or lavender; calyx lobes, pedicels, and peduncles pallid to pinkish-tinged, drying brown; mostly inland from Baja California to the Cascade Range of southern Washington.

Corolla lips whitish to pinkish (reddish brown in herbarium specimens); corolla tube broad, 4 mm or more in diameter at the constriction and gradually widening toward the throat; montane in Baja California and Southern California to Ventura and Kern Cos. lf. ssp. *jeudgei*

Corolla lips white or yellowish to pinkish (sometimes purplish-tinged in herbarium specimens); corolla tube slender below, usually less than 4 mm in diameter at the constriction and abruptly expanding distally toward the widely spreading lips.

Corolla 35–40 mm long; throat of corolla 10 mm or more in diameter; lower lobes of corolla lance-ovate, 5 mm or more broad; mostly near the coast, Los Angeles to San Luis Obispo Cos. le. ssp. *grandis*

Corolla 25–35 mm long; throat of corolla less than 10 mm in diameter; lower lobes of corolla lance-subulate to lance-oblong, usually less than 5 mm broad.

Plants usually longer than 10 cm; stem below the inflorescence 6 cm or more long; inflorescence racemose to paniculate; racemes 5–20 cm long; Central Valley of California and surrounding mountains to 3,000 m; occasionally in the Coast Ranges and their valleys. lc. ssp. *jepsonii*

Plants usually less than 10 cm long; stem below the inflorescence usually less than 6 cm long; inflorescence of subcorymbose or subcapitate clusters mostly less than 6 cm long.

Stem below the inflorescence usually less than 3 cm long; lower lobes of corolla lance-subulate, less than 3 mm broad near base, with acute and pointed apex; meadows of the Sierra Nevada and Cascade Range from Tuolumne Co., California, N to Klickitat Co., Washington; occasional in lowland meadows. lb. ssp. *grayana*

Stem below the inflorescence 3–6 cm long, lower lobes of corolla 3 mm or more broad, lance-oblong to narrow-triangular, with the apex blunt-acute or obtuse; South Coast Ranges from northern Santa Barbara Co. N to southern Santa Clara Co., California. ld. ssp. *condensa*

1a. OROBANCHE CALIFORNICA C. & S. ssp. CALIFORNICA.

Aphyllon violaceum Eastw., Zoe 5:85. 1900. *Myzorrhiza violacea* (Eastw.) Rydb., Bull. Torrey Bot. Club 36:695. 1909. *Orobanche comosa* var. *violacea* (Eastw.) Jeps., Man. Fl. Pl. Calif. 952. 1925. *Orobanche grayana* var. *violacea* (Eastw.) Munz, Bull. Torrey Bot. Club 57:616. 1931. TYPE: California: Marin Co.: Vision Hill, W of Tomales Bay, *Eastwood s.n.*, 1 Sep 1900. (HOLOTYPE: CAS!; ISOTYPE: UC!)

Orobanche grayana var. *nelsonii* Munz, Bull. Torrey Bot. Club 57:616. 1931. TYPE: Oregon: Marion Co.: one mile N of Salem, *J. C. Nelson 2479*. (HOLOTYPE: GH!)

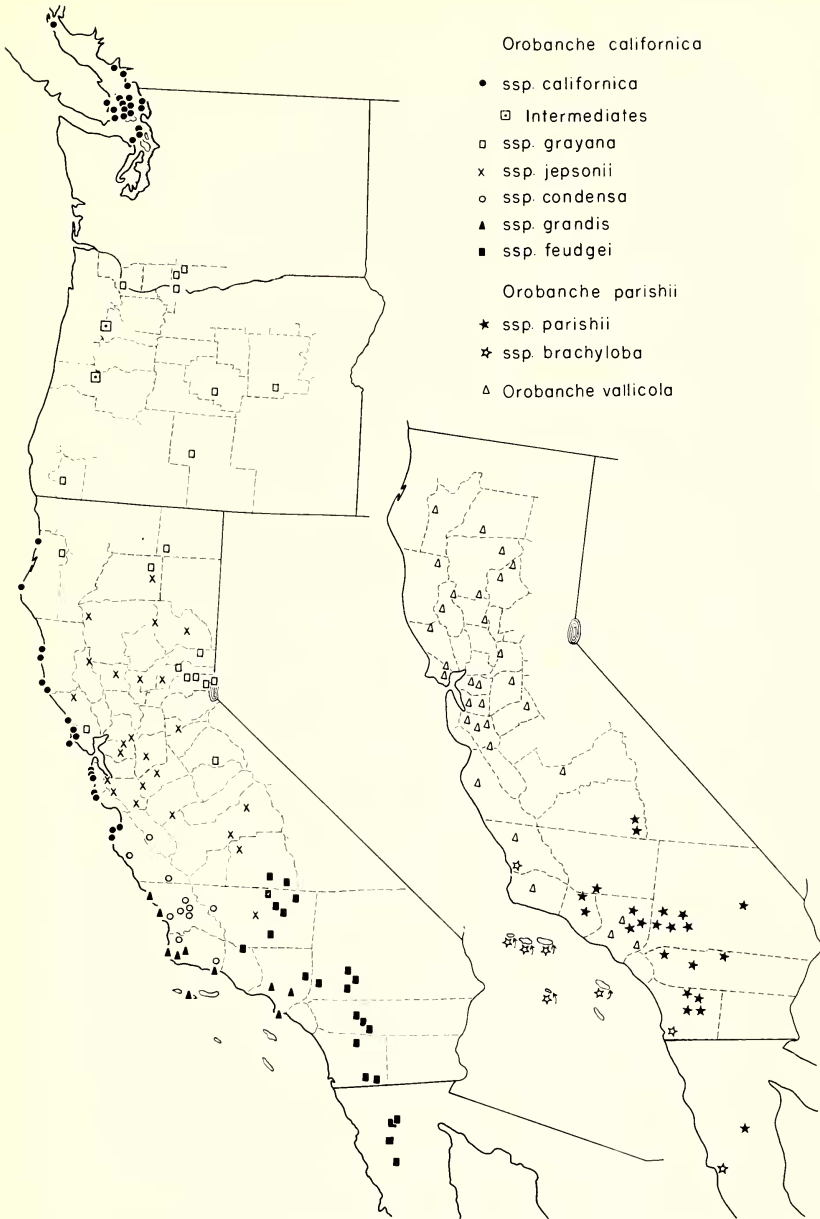


FIG. 5. Distribution of *Orobanche californica*, *O. parishii*, and *O. vallicola* in western Canada, Mexico, and the United States.

Plants 5–20 (27) cm long; stems simple or fastigiate branched, the flowers borne in subcorymbose or subcapitate (rarely subspicate) clus-

ters up to 8 cm long; lower pedicels rarely over 1 cm long; calyx lobes 6–15 (20) mm long, usually dark purple; corolla (22) 25–40 (45) mm long, the lobes purplish, sometimes paler externally, the tube fading to whitish or pale yellow; corolla tube conspicuously widening toward throat, the throat 8–10 mm broad; lobes of upper lip oblong-ovate, their apices broadly obtuse (less commonly acute), shallowly retuse, or erosulate; lobes of the lower lip lanceolate to oblong, 8–12 (18) mm long, their apices acute to obtuse; stigma bilamellate with spreading or revolute lobes, occasionally becoming crateriform.

Hosts: Frequently reported on *Grindelia* spp.; also reported on *Erigeron glaucus* in Mendocino Co., Calif. (*Daniels*, 1 Sep 1965; *Roderick*, 10 Sep 1961).

DISTRIBUTION: Rare and possibly extinct in meadows of the Willamette Valley, Oregon; occasional on rocky banks and on sandy flats and slopes near the sea in SW British Columbia and in NW Washington on the San Juan Islands and occasionally on the neighboring mainland; occasional in sandy or gravelly soil of coastal bluffs along the California coast from Big Lagoon, Humboldt Co., S to the Monterey Peninsula. Jun–Oct. Known localities (fig. 5):

BRITISH COLUMBIA: Bowen Island, Eagle Cliff, *McBride*, 2 Aug 1964 (UBC); Vancouver, Locarno Park, *Eastham 5683* (UBC); Mitlenatch Island, Georgia Strait, *Fowle*, 26 Jun 1961 (V); Vancouver Island, Parksville, *Taylor 3163* (UBC); Genoa Bay, N side of Cowichan Bay, *Wollaston*, 9 Jun 1927 (V); Saanichton, *Taylor 3038* (UBC); Oak Bay, Victoria, *Newcombe*, 16 Jun 1924 (WS); Beacon Hill, Victoria, *Macoun*, 14 Jul 1887 (NY, US); South Pender Island, *Szczawinski*, 2 Sep 1955 (UBC, V).

WASHINGTON: SAN JUAN CO.: Sucia Island, *Flett 2755* (WS); Flat Top Island, *Lawrence 103* (UC, WS, WTU); Orcas Island, *Eyerdam*, 4 Jul 1935 (UC, UWT); Shaw Island, *Zeller 890* (NY, US); Wasp Island, *Foster*, 25 Jun 1904 (WS); San Juan Island, Friday Harbor, *Frye*, 25 Jun 1904 (WS). WHATCOM CO.: Lummi Rocks, *Muenschner 8362* (MO, UC, UTS, WS). SKAGIT CO.: Vandovia Island, *St. John 7910* (WS); Northwest Island, Deception Pass State Park, *Smith 1158* (UWT, WS). ISLAND CO.: Whidbey Island, Oak Harbor, *Smith 1389* (DS). JEFFERSON CO.: Port Townsend, *Otis 2350* (DS, UC, WS, WTU).

OREGON: [both collections transitional to ssp. *grayana*] MARION CO.: 1 mi N of Salem, *Nelson 2940* (GH, WS). LANE CO.: Eugene City in 1873 [collector's name not readable] (GH).

CALIFORNIA: HUMBOLDT CO.: Big Lagoon, *Tracy 6761* (JEPS, UC, UTC); 3 mi S of Cape Mendocino, *Tracy 4970* (JEPS, UTC). MENDOCINO CO.: Fort Bragg, *Eastwood 1639* (CAS, GH); Mendocino City, *Daniels*, 1 Sep 1965 (JEPS); 1½ mi SE of Point Arena lighthouse, *Alava*, 5 Oct 1957 (JEPS); ca 1 mi N of Anchor Bay, *Roderick*, 10 Sep 1961 (JEPS). SONOMA CO.: just N of mouth of

Salmon Creek, *Jepson 15950* (JEPS). SAN MATEO CO.: San Pedro, *K. Brandegee* (UC 217609); Farallone City, *Setchell 173* (F, GH, MO, RM, UC); Pillar Point, N end of Half Moon Bay, *Newlon 68* (DAO, JEPS, UC, UTC); near Pebble Beach 1½ mi S of Pescadero Creek, *Hesse*, 30 Jul 1954 (JEPS); Pigeon Point, *Mason 3983* (JEPS, UC, UTC.) MONTEREY CO.: Seaside Station near Monterey, *K. Brandegee* in 1910 (UC); Pacific Grove, *Dudley*, 27 Jun 1905 (DS); S side of Pt. Lobos State Park, *Wilson*, 5 Oct 1937 (UC).

Plants assigned to this subspecies form a fairly discrete and easily recognizable group throughout most of their range. The deep purplish corolla and calyx are unique to these plants in the complex and the maritime habitat common to most of them is shared within their range only by a distinctive undescribed species at San Francisco and southward. The preference of ssp. *californica* for *Grindelia* as a host seems to be a strong one. *Grindelia* is the principal host for only one other subspecies, *O. californica* ssp. *jepsonii* of central California.

Morphological variation within this taxon is only partially correlated with geography. Along the central California coast (Monterey Peninsula north to Pt. Reyes, Marin Co.) the plants mostly have large (35–45 mm long) and broad, deep purple corollas with correspondingly long lips (12–16 mm) and with upper lobes that are broad and rounded at the apex. Munz (1930) referred these plants to *O. grayana* var. *violacea*. There are, however, at the northern and southern extremes of this distribution plants (*Dudley s.n.*, Monterey Co.) that have somewhat smaller (25–35 mm long) and narrower corollas, often with the upper corolla lobes pointed. These plants sometimes have a pale lavender corolla and match quite closely the plants of Humboldt Co. and the Pacific Northwest that were recognized by Munz (1930) as *O. grayana* var. *nelsonii*. This variety was partially sympatric with var. *violacea* and was parasitic on plants belonging to the same host genus. There is no sharp line separating the large-flowered plants from the smaller-flowered ones.

The small-flowered plants of the subspecies are variable in the shape of the stigma and, occasionally, in anther indument. Whereas the stigma of the large-flowered plants is usually bilamellate with thin, spreading, triangular lobes, the stigma in small-flowered plants (Monterey Peninsula, Humboldt Co., and the Pacific Northwest) ranges from small and thin, bilamellate lobes to a thicker, more crateriform type (fig. 4, A). There is no apparent correlation of stigma type with geography. Further complicating construction of identification keys within the *O. californica* group is a variability within this subspecies in density of anther hairs ranging from densely villous (the usual condition) to occasionally nearly glabrous in northern California (*Tracy 6761*, Humboldt Co.).

In the northern distribution of ssp. *californica*, range disjunctions and morphological variants are evident. The plants of the San Juan Islands and vicinity are similar to the small-flowered plants of California in all

respects. Rather similar plants again appear in an inland habitat nearly 320 km distant at Salem, Oregon, growing on *Grindelia*. Judging from herbarium specimens, the corollas are paler and the plants are mostly smaller than the San Juan Island plants, but otherwise the resemblance is close. The Salem plants collected in 1918 and 1919 are the last record in the Willamette Valley region. One would expect the type of *O. comosa* Hook. (a later homonym, renamed *O. grayana* by Beck) collected by David Douglas from the Fort Vancouver area to be similar to the Willamette Valley plants, but only one specimen (fig. 6, D) of four on the holotype sheet (fig. 6, A–D) shows the purplish color of corolla and calyx lobes characteristic of ssp. *californica*. The remaining three plants have a closer resemblance to the reduced, subcorymbose plants with light corollas that occur to the east in mountain meadows (see discussion of ssp. *grayana*). Willamette Valley plants are shown as intermediate between the two subspecies since the plants are mostly smaller and the inflorescence parts somewhat lighter than those of the San Juan Islands (fig. 5).

1b. **Orobanche californica** ssp. **grayana** (Beck) Heckard, stat. et comb. nov.

Orobanche grayana G. Beck, Bibl. Bot. 4(19):79. 1890. *Myzorrhiza grayana* (Beck) Rydb., Bull. Torrey Bot. Club 36:695. 1909. Based on: *O. comosa* Hook., Fl. Bor. Am. 2:93. 1838 (not *Orobanche comosa* Wallroth, Sched. Critic. 1:314. 1822). *Anoplantus comosus* (Hook.) Walp. Repert. Bot. 3:480. 1844. *Phelipaea comosa* (Hook.) A. Gray, Pac. R.R. 4:118. 1857. *Aphyllon comosum* (Hook.) A. Gray, Bot. Calif. 1:584. 1876. TYPE: "Banks of the Columbia, Douglas, Scouler, . . ." (LECTOTYPE: K!; Photograph, UC; see discussion below.)

Plants 4–10 cm in length with short (1–5 cm) stems; inflorescence subcorymbose, few to many-flowered; calyx lobes pallid to occasionally purplish, the lobes (7) 9–13 (16) mm long; corolla (25) 28–33 mm long with widely spreading lips 10–12 mm long, dull white or yellowish to pinkish or pale lavender, often with lavender veins; lower lobes of corolla lanceolate to lance-subulate, pointed, the upper lobes rounded to pointed; stigma thin, bilamellate.

HOSTS: Reported frequently on *Erigeron* and *Aster* and occasionally on grasses.

DISTRIBUTION: Meadows and stream margins, mostly 1,200–1,800 m in California, descending to about 450 m in the Cascade Range of southern Washington; occasionally near sea level. Cascade-Sierra Nevada ranges from Klickitat Co., Wash., S to Tuolumne Co., Calif.; occasionally in the Coast Ranges (S. Oregon and Central California) and mountains of the Columbia Plateau in Oregon. Jun–Oct. Known localities (fig. 5):

WASHINGTON: KLICKITAT CO.: Falcon Valley, *Suksdorf*, 15 Sep 1882 (F, GH, NY, UC, WS); Gilmer, *Suksdorf* 7354 (WS). CLARK

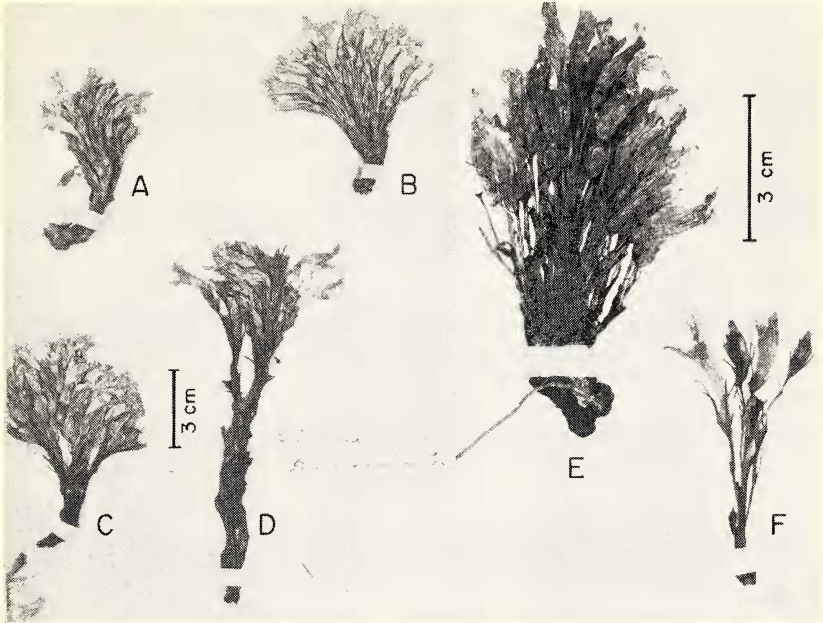


FIG. 6. *Orobancha californica* ssp. *grayana*: A-D, Holotype sheet (Douglas, Scouler) of *O. grayana*. E-F, Douglas collection (presumably No. 386) from vicinity of Fort Vancouver.

CO.: Fort Vancouver, *D. Douglas* 386 (K).

OREGON: HOOD RIVER CO.: Hood River Valley, *Henderson*, 8 Sep 1896 (RM). GRANT CO.: below Pine Spring on N branch of Grasshopper Creek, *Abbott* 3 (WS). CROOK CO.: W of Drake Butte, *Brats* 58 (OSC). LAKE CO.: Summer Lake, *Clark*, Aug 1911 (WILL). JOSEPHINE CO.: lower Illinois River road, *Barnes*, 11 June 1957 (OSC) [atypical in having dark calyx lobes and bracts].

CALIFORNIA: HUMBOLDT CO.: Oregon Creek, Salmon Mts., *Nichaus* 934 (JEPS). MODOC CO.: Egg Lake, *Nutting*, Aug 1915 (UC). SHASTA CO.: Pit River near mouth of Fall River, *Newberry*, 5 Aug 1895 (GH). PLUMAS CO.: Big Meadows, *Austin* in 1879 (SD). SIERRA CO.: Sierra Valley, *Lemmon* in 1874 (JEPS). NEVADA CO.: Loneys Meadow, Bowman Lake area, *Mott*, 22 Sep 1963 (CAS). PLACER CO.: near Summit, *Schreiber* 764 (UC); near Cisco, *Mason* 7177 (UC); Brockway, *Hall & Chandler* 4551 (UC); Tahoe Tavern, Lake Tahoe, *Beans*, 7 Sep 1914 (GH, JEPS). TUOLUMNE CO.: Miguel Meadow, Yosemite National Park, *Mason* 12127 (UC, JEPS). SONOMA CO.: Laguna, Chileno Valley, *Rubtzoff* 6615 (JEPS).

NEVADA: WASHOE CO.: near Reno, *Henning* (NY).

No previous attempt has been made to establish the type specimen and its precise geographic origin for *Orabanche grayana* Beck (based on *O. comosa* Hooker, a later homonym). Hooker's protologue states, "Hab. Banks of the Columbia. Douglas, Dr. Scouler, Dr. Gairdner." Of two possible type sheets (at Kew) collected by David Douglas, one is labeled in Hooker's hand, "Columbia—Douglas, Scouler", and the other is labeled in an unknown hand, "Alluvial grassy plains, Ft. Vancouver". Gairdner's material, which would have been collected in 1833 (McKelvey, 1955), several years after Douglas's, was not represented at Kew. The original drawing of one plant that accompanied the description of *O. comosa* Hook. was pinned to the "Douglas-Scouler" sheet. The drawing best matches the lower left-hand specimen (fig. 6, C) in habit, although the unusual retuse apices of the lower corolla lobes of the original drawing could not be found on any plants of this sheet. Some corollas showing this retuse apex on the lower lobes were found on the Douglas "Ft. Vancouver" collection (fig. 6, E, F), but the two upper lobes were also retuse, a feature not shown in the drawing. I have concluded that the original diagnosis and drawing are composite, not completely accurate for any one specimen, and I have selected the lower left-hand specimen (fig. 6, C) of the "Douglas-Scouler" collection as the lectotype.

The probable collecting locality for the "Douglas-Scouler" specimen can be determined since those two collected together only in April-May and September of 1825 and only in the vicinity of Ft. Vancouver (McKelvey, 1955).

There is a close relationship and intergradation between ssp. *grayana* and ssp. *californica* in the Willamette Valley-Columbia River region of Oregon and southern Washington, and the occurrence of the type collection of *O. grayana* within this region makes identifications critical. Few collections are available and the enormous urban and agricultural developments since the last collection near Salem in 1919 discouraged further search for the plants. The morphological differences of the few available specimens suggest a taxonomic treatment that recognizes the presence of features of both subspecies, mostly those of *grayana* for the Fort Vancouver plants and of *californica* for the collections from Salem and Eugene. The latter clearly show the purple corolla and dark purplish calyx characteristic of ssp. *californica*, although the color appears to be less intense than in the coastal plants. The host for the Salem plants agrees with that of the coastal plants. The collections of Douglas's, on the other hand, largely lack this coloration. Only one plant (from the type sheet, fig. 6, D) has a purple corolla and calyx, and it is also taller (14 cm) than any specimens of ssp. *grayana*. The other specimens of the Douglas collections are short subcorymbose plants with a light calyx and corolla quite like the plants of montane meadows about 100 km eastward in Klickitat Co. (*Suksdorf* 7354). That the present pallid appearance of the Douglas collections is not a deception due to age is

verified by the excellent description by Douglas (1914) in his published diary for his number 386 from near Fort Vancouver: "flowers white, mixed with rose color, sometimes sulphur-yellow where very much shaded". The sheet (fig. 6, E, F) at Kew labeled "Alluvial grassy plains, Fort Vancouver 1825" is presumably Douglas's number 386 (although it is not so labeled).

The present circumscription of this taxon differs from previous interpretations (Munz, 1930; Ferris, 1960) in that the group is here largely limited to the reduced, montane plants with light-colored corollas (white to pale pinkish, often with lavender veins). My interpretation extends the geographic circumscription beyond these montane plants to include three collections from lowland areas. The first two are David Douglas's collections, including the type of *O. grayana*, that were made west of the Cascade Range in the vicinity of Ft. Vancouver. The montane plants at this latitude are at an elevation of only about 450 m and the presence of the plants farther down the Columbia River at a lower elevation could be explained as a chance establishment of seed from a higher elevation. The other collection from a lowland region is from vernal wet ground in Chileno Valley, Sonoma Co., Calif. (*Rubtzoff 6615*) at an elevation of about 60 m. They were in a region in which ssp. *jepsonii* would have been expected but were considerably smaller and had the corymbose inflorescence of *grayana*. Also, the plants were growing on *Aster*, a genus frequently reported as a host for *grayana* but not for *jepsonii*. Other boreal and montane plants also appear in these cold, marshy areas of the northern California coastal region, including *Menyanthes* (Baker, 1972) and several examples cited by Rubtzoff (1953), who suggests that cooler temperatures brought about by the influence of cool, moist ocean air account for the occurrence of these plants.

Plants of ssp. *grayana* are the most highly reduced plants of the species and, except for the striking difference in habit, are much like those of *jepsonii* of central California, which are postulated to be their nearest relatives. Specimens that appear intermediate are rare but the following occur: Shasta Co., Calif., at 2,800 ft. (*Newberry* in 1855); Butte Co., Calif., at 5,200 ft. (*Copeland*, 13 Sep 1938); Oregon Rogue River at Woodville, (*T. Howell*, 14 Aug 1888, ORE).

1c. ***Orobanche californica* ssp. *jepsonii*** (Munz) Heckard, stat et comb. nov.

Orobanche grayana var. *jepsonii* Munz, Bull. Torrey Bot. Club 57:617. 1931. TYPE: California: Colusa Co., Princeton, *H. P. Chandler*, Oct 1905 (HOLOTYPE: POM!; ISOTYPE: UC!).

Plants (8) 10–35 cm in length; stems 6–15 cm long below the inflorescence, simple or branched either basally or along the lower half of stem; inflorescence paniculate to racemose, 5–20 cm long; flowers mostly pedicellate, the pedicels decreasing in length upwards in the inflorescence; calyx lobes pallid or pinkish tinged, subulate to linear-subulate,

(8) 10–20 (25) mm long; corolla (25) 30–35 (40) mm long, whitish or pale yellowish brown to pinkish, often with the veins of the lips deep rose or purplish, the tube conspicuously widened toward the throat; corolla lips widely spreading, 10–12 (15) mm long, the lower lobes mostly narrow-lanceolate and pointed, the upper lobes deltoid with acute and often erosulate or emarginate apices; anthers densely villous, 1.5–2.0 mm long; stigma thin, bilamellate with triangular spreading lobes.

HOSTS: *Grindelia* (Brewer 1260, UC; Roderick, 8 Jul 1967; S. Smith 2658; *Stinchfield* 451), *Baccharis viminea* (Chandler holotype), *Rubus vitifolius* (Jepson 5157), *Chrysothamnus* (Munz 22295).

DISTRIBUTION: Bottomlands and dry hillsides up to 3,000 m. Central Valley and surrounding mountains from the Cascade Range of Shasta and Plumas counties S in the Sierra Nevada to Kern Co.; central California Coast Ranges from Tehama to Santa Cruz counties. May–Oct. Known localities (fig. 5):

CALIFORNIA: SHASTA CO.: Hat Creek, Signal Mt. station, Kramer in 1937 (CAS). PLUMAS CO.: below Mt. Ingalls Lookout, N of Grizzly Valley, 7,800 ft., Balls 15630 (RSA). BUTTE CO.: Jonesville, Copeland, 13 Sep 1938 (UC) [transitional to ssp. *grayana*]. YUBA CO.: Marysville, Bigelow, 25 May 1854 (GH). NEVADA CO.: 1 mi NE of Wolf Mt. (6 mi SW of Grass Valley), Roderick, 8 Jul 1967 (JEPS). COLUSA CO.: Colusa-Williams road, Stinchfield 451 (DS). AMADOR CO.: Pine Grove, Hansen 247 (UC). FRESNO CO.: Kaiser Crest, 9,800 ft., Jepson 13,010 (JEPS); bank of Kings River, 2–3 mi NW of Reedley, Quick 52–350 (CAS); N of Oro Loma, Lyon 570 (UC). TULARE CO.: Visalia, Congdon, Sep 1881 (DS). KERN CO.: 0.5 mi W of Pyramid Hill, Weston 697 (CAS). TEHAMA CO.: 0.5 mi E of summit of South Yolla Bolly Mt., Tucker & Mann 3554 (DAV). LAKE CO.: Snow Mt., Munz 22295 (RSA). SONOMA CO.: Duncan Mills, M. Jones, 18 Jul 1882 (POM). SOLANO CO.: Haas Slough, N of Rio Vista, Jepson, 8 May 1885 (JEPS). CONTRA COSTA CO.: Antioch, T. Brandegee, Jun 1884 (UC); Mt. Diablo, Elmer 4958 (UC). SAN JOAQUIN CO.: San Joaquin Bridge near Lathrop, T. Brandegee, 9 Sep 1901 (UC). STANISLAUS CO.: 9 mi W of Modesto, S. G. Smith 2658 (JEPS); Cañada del Puerto, near Mt. Oso, Brewer 1273 (GH, UC). SANTA CLARA CO.: Palo Alto, Dudley, 14 Sep 1901 (DS); trail from Madrone Springs to Gilroy Hot Springs, Dudley, 31 May 1895 (DS); Saratoga, Jepson 5157 (JEPS).

The circumscription of this subspecies followed here is similar to that proposed by Munz (as *O. grayana* var. *jepsonii*) except that it has been broadened to include several collections of montane (elevation 1,500 to nearly 3,000 m) plants that heretofore have remained undetermined. These montane plants are sometimes highly reduced (Fresno Co.: Jepson 13,010; Tehama Co.: Tucker & Mann 3554) and thus resemble ssp. *grayana* in size and corymbose inflorescence. They have a more deeply colored corolla (and sometimes calyx) than ssp. *grayana*, how-

ever, and occur in dry, rocky habitats, as do some *jepsonii* of the lower foothills, rather than in moist meadows, as does ssp. *grayana*. Not all these montane plants are reduced and two collections (Shasta So.: *Kramer* in 1937; Plumas Co.: *Balls 15630*) are much like lowlands plants of *jepsonii* in size and habit. There might be some value in creating another subspecies to accommodate these montane plants, but their infrequent and widespread distribution suggests that they are montane variants of *jepsonii* in each region rather than a cohesive genetic entity.

There is intergradation with neighboring subspecies. Thus, some specimens from Santa Clara Co. (as *Dudley*, 31 May 1895) appear to be intermediate towards ssp. *condensa*. Other specimens (*T. Brandegee* in 1884; *Jepson*, 8 May 1885) of the lower delta region of Contra Costa and Solano counties have purple corollas similar to those of ssp. *californica*. Intergradation with ssp. *grayana* is discussed under that subspecies. Identification of ssp. *jepsonii* is complicated by the close relationship to *O. vallicola*, with which it is largely sympatric. This aspect is discussed further under *O. vallicola*.

1d. ***Orobanche californica* ssp. *condensa*** Heckard, ssp. nov.

TYPE: California: San Luis Obispo Co.: along Yaro Creek, 7½ mi (12 km) N of Pozo, 1,600 ft. (470 m) elevation, *Bacigalupi, Ferris, & Robbins 5242*, 25 May 1955 (HOLOTYPE: JEPS!; ISOTYPES: NY!, RSA!, US!, WTU!).

Plantae 5–10 (15) cm altae caulibus strictis vel parce fastigiato-ramosis, inflorescentiae pleurumque minus quam 25 floribus subcapitatae vel subcorymbosae; corolla 25–35 mm longa, labii superioris superficie interiore pleurumque rubropurpurata, venis profundius purpureis, labio inferiore albido, purpureotincto, plerumque venis purpureis obsito; corollae faux ca 6 mm lata, tubo lato ad faucem versus parum dilatato; corollae labia 8–10 (12) mm longa, lobis rotundatis vel apice obtusato acutis.

Plants 5–10 (15) cm in length; stems simple or sparingly fastigiately branching, 3–8 (12) cm long, the flowers borne at the top in subcapitate or subcorymbose clusters; calyx 10–16 (20) mm long, the lobes linear-subulate; corolla 25–35 mm long, sordid white to yellowish or brownish externally, the upper lip mostly uniformly reddish-purple on the inner surface with darker purple veins, the lobes of lower lip whitish, purplish tinged, or purple-veined; corolla throat ca 6 mm broad, the tube broad and widening slightly toward throat; corolla lips 8–10 (12) mm long, the lobes of upper lip 2–4 mm long, broadly oblong, their apices obtuse, rounded, rarely acute, often erosulate, or emarginate; lobes of lower lip bluntly acute or obtuse, often retuse or emarginate; stigma bilamellate with triangular lobes.

HOST: *Chrysoopsis villosa* (several collections).

DISTRIBUTION: Sandy or gravelly soil, 150–500 m, in California in South Coast Ranges from San Benito to Santa Barbara counties. May–Jul. Known localities (fig. 5):

CALIFORNIA: SAN BENITO CO.: Vancouver Pinnacles, *I. Smith*, 18 Jun 1914 (JEPS). MONTEREY CO.: Tassajara Hot Springs *Elmer 3240* (DS); W of Bradley, *Hardham 10781* (RSA). SAN LUIS OBISPO CO.: Cammatti Canyon, 11 mi S of Shandon, *Bacigalupi et al. 5128* (JEPS); Black Mt., *Hardham 774* (JEPS); 2 mi S of Huerhuero school, *Lee 1055* (UC); San Luis Obispo, *Condit*, 7 Jun 1910 (UC). KERN CO.: Temblor Mts., *Hardham 758* (CAS) [aff. ssp. *feudgei*]. SANTA BARBARA CO.: Blochmans Ranch near Santa Maria, *Eastwood 479* (CAS); Santa Ynez Mts. toward San Rafael Mts., *H. Ford*, ca 1895 (SBM).

This subspecies accommodates a fairly distinct phase that replaces ssp. *jepsonii* in a region peripheral to the range of the latter. The plants are closest in affinity to those of ssp. *jepsonii* and ssp. *grandis*, differing from them in their smaller stature, in having fewer flowers in a more congested subcorymbose or subcapitate inflorescence, and in having a slightly smaller corolla, often with deeper purplish-red upper lip lobes. A difference in host preference is suggested by the report of only one host, *Chrysopsis villosa*, for 6 collections.

Intergradation of ssp. *condensa* with neighboring subspecies is present. A collection (*Dudley*, DS 10395) from Santa Clara Co. assigned to ssp. *jepsonii* has a short raceme and a large corolla with rather deep reddish purple lips, features that indicate that it is intermediate morphologically between the two subspecies. The plants also occupy an intermediate position geographically. In San Luis Obispo Co. a collection of *Hardham's (774)* has the broader corolla tube reminiscent of ssp. *feudgei* or ssp. *jepsonii*, and another collection (*Hardham 758*) in the Temblor Mts. of Kern Co. is even further removed morphologically from ssp. *condensa* and is an intermediate link, both morphologically and geographically, with ssp. *feudgei*.

G. Thomas Robbins of the Jepson Herbarium first recognized the distinctness of these plants and had proposed a manuscript name that suggested that the plants were confined to or typical of San Luis Obispo Co. Since this subspecies also occurs in several other counties, I have chosen a name that points out the reduction in size of stem, inflorescence, and flower from that of its nearest relatives.

1e. ***Orobanche californica* ssp. *grandis*** Heckard, *ssp. nov.*

TYPE: California: Santa Barbara Co.: dunes at Surf, *H. M. Pollard*, 22 Jul 1954 (HOLOTYPE: UC!; ISOTYPE: CAS!).

Plantae 8–30 cm altae, caulibus simplicibus vel numerosis fastigiatisque; inflorescentia subcorymbosa, interdum subracemosa; corolla 35–50 mm longa, fauce 9–10 mm lata, gradatim in tubum diam. 4 mm angustata; corollae labiis late oscitantibus, 12–14 mm longis, lobis superioribus latis obtusisque, eis inferioribus lanceolatis vel lanceolato-ovatis, angustatis sed apicis obtusatis.

Plants 8–30 cm long, the stems single or numerous and fasciculate,

(5) 10–20 cm long below the inflorescence, 5–18 mm thick, usually unbranched below; flowers borne in subcorymbose or occasionally subspicate clusters; calyx lobes 15–20 mm long; corolla 35–50 mm long, the tube buff or yellowish with the lips pinkish or pale brownish-red with darker veins (rarely the entire corolla pallid or yellowish); corolla throat 9–10 mm broad, the upper tube tapering to a sinus ca 4 mm in diameter; corolla lips widely spreading, 12–14 mm long, the upper corolla lobes broad and obtuse; lower corolla lobes lanceolate to lanceovate, acute with blunt apices; stigma bilamellate with triangular lobes.

Hosts: Reported on *Haplopappus venetus* var. *vernonioides* at Surf, Santa Barbara Co. (Pollard in 1954; Carlquist 241, UC), *Adenostoma fasciculatum* (Norris, UCLA), *Artemisia* (Brewer 399), *Heterotheca* (Kimble, 25 May 1961).

DISTRIBUTION: California, sandy soil of dunes, bluffs, and canyons near the coast from San Luis Obispo to Los Angeles counties. Santa Rosa Island. Rare. Apr–Oct (Nov). Known localities (fig. 5):

CALIFORNIA: SAN LUIS OBISPO CO.: ca 1 mi N of Cambria Pines, *H. M. Beard*, 29 Nov 1959 (JEPS); SW end of Morro Bay, *Barnes*, 5 Sep 1960 (SBBG); near Nipomo, *Kimble*, 25 May 1961 (CDA). SANTA BARBARA CO.: head of Mission Canyon, ca 6 mi NE of Lompoc, *Wood*, 20 May 1946 (SBM); Foxin's [Foxen's] Ranch, near Los Alamos, *Brewer 399* (GH); Montecito, *Riedel*, Oct 1928 (SBM); Santa Rosa Island, *Hoffman*, 11 Jun 1930 (SBM). LOS ANGELES CO.: summit of Laurel Canyon road, Santa Monica Mts., *Griesel*, 18 Jun 1936 (LA); Portuguese Bend, *Norris*, 1 Apr 1968 (LA); East Los Angeles, *Abrams*, 13 Jul 1906 (DS) [aff. ssp. *feudgei*].

The plants assigned to this subspecies have been variously identified in the past. The northern coastal specimens from Surf and Cambria were aligned with ssp. *californica*, whereas the southern collections were identified as ssp. *jepsonii* or ssp. *feudgei*. These identifications were due in part to a variation pattern within the subspecies that is partially geographically correlated. The northern populations have purplish corolla lips that are lighter but similar to those of ssp. *californica* of the central California coast and northward. The more southerly populations of ssp. *grandis* have a lighter corolla that is similar to that of ssp. *jepsonii* and a broader corolla that is similar to that of ssp. *feudgei*. None of these variants, however, fits comfortably into these other subspecies, and ssp. *grandis* is proposed to encompass these closely related populations that share a unique combination of features of habit and corolla size and shape.

The closest relationship of ssp. *grandis* is probably with ssp. *californica*, which occupies similar coastal habitats to the north. A gap of 250 km in their known ranges separates the extremes of the two subspecies. The most northern collection assigned to ssp. *grandis* (*Beard*, 29 Nov 1959) is somewhat intermediate between the two subspecies in habit and corolla color. There are no obvious intergrades between ssp. *grandis*

and ssp. *condensa* although their ranges are close. Slight differences in elevation and habitat, and possibly in host preference, separate these subspecies. Likewise, ssp. *feudgei* is apparently separated from ssp. *grandis* by differences in elevation and habitat and host preference. A specimen from East Los Angeles (*Abrams*, 13 Jul 1906), probably collected below 250 m elevation, strongly resembles ssp. *feudgei* and I have identified it as intermediate towards this subspecies.

1f. ***Orobanche californica* ssp. *feudgei*** (Munz) Heckard, comb. et stat. nov.

Orobanche grayana var. *feudgei* Munz, Bull. Torrey Bot. Club 57:616. 1931. TYPE: California: San Bernardino Co.: dry, rocky slope above Baldwin Lake, San Bernardino Mts., 7,500 ft., *Munz 8177* (HOLOTYPE: POM!).

Plants 1–3 dm long, stems (6) 10–18 cm long below the inflorescence, up to 2 cm thick, usually unbranched below, the flowers borne in a subcapitate or subcorymbose cluster, or occasionally in a raceme to 12 cm long; calyx lobes (12) 15–20 (23) mm long; corolla 25–35 mm long, whitish or yellowish to pale rose with darker veins, commonly on drying appearing reddish to brownish red; corolla throat 8–10 mm wide, the upper tube broad and gradually tapering to the sinus; corolla lips (8) 10–12 mm long, the upper corolla lobes broadly oblong and rounded with the apex sometimes emarginate or shallowly retuse, slightly spreading and sometimes reflexed; lower corolla lobes narrowly oblong, subacute or obtuse, sometimes shallowly retuse at apex, usually spreading; stigma bilamellate with triangular lobes.

HOST: *Artemisia tridentata*.

DISTRIBUTION: Washes and open sagebrush flats and slopes. California, from the Kern Plateau of Tulare Co. and the vicinity of Mt. Pinos in Ventura Co. S through the mountains of SW California to the Sierra San Pedro Martir in Baja California; 750–2,500 m. Not common May–Jul. Known localities (fig. 5):

CALIFORNIA: TULARE CO.: S side of Sherman Peak, *Twisselmann & McMillan 14676* (CAS); N end of Long Valley, Kern Plateau, *Howell & True 42817* (CAS). KERN CO.: 5.9 mi E of summit, Greenhorn Mt., *Hardham 2198* (CAS); ridge N of Liepel Peak, Piute Mts., *Breedlove 3874* (CAS, DS); 3.6 mi W of Claraville, Piute Mts., *Breedlove 4010* (CAS, DS); Walker Pass, *Rose*, 10 May 1940 (CAS); top Biss Peak, Tehachapi Mts., *Dudley 393* (DS). VENTURA CO.: Stauffer, Mt. Pinos, *Hall 6327* (UC). LOS ANGELES CO.: Swartout Canyon, San Gabriel Mts., *Abrams & McGregor 654* (DS). SAN BERNARDINO CO.: Lytle Creek canyon, San Antonio Mts., *Hall*, 1–3 Jun 1900 (UC); 37 mi SE of Victorville, San Bernardino Mts., *Holmgren & Reveal 2598* (BRY); S. Fk. Santa Ana River, 6,200 ft., *Grinnell*, 27 Jun 1907 (US). RIVERSIDE CO.: Van Deventer's [Santa Rosa Indian Reserv.], San Jacinto Mts., *Jepson 1458* (JEPS); near Hemet Lake,

Keator, 17 May 1959 (UCSB); S slopes Santa Rosa Mts., *Munz 5827* (UC). SAN DIEGO CO.: 5½ mi NW of San Luis Rey River Bridge on highway 79, *Weiler & Taylor 61123* (JEPS); mountains near Jacumba, *Northrup*, 7 May 1935 (UC); Boulevard, *McGregor*, 18 May 1919 (DS).

MEXICO: BAJA CALIFORNIA: near Hanson's Ranch, *Orcutt*, 27 Jul 1883 (UC); 1 mi W of El Rayo, *Moran 18470* (SD); 1 mi NE of Rancho el Florido, *Moran 17737* (SD); Aliso, *T. Brandegee*, 30 May 1893 (UC).

The plants with the morphological features defining ssp. *feudgei* correlate fairly well with a distinct ecology and geography. Host records list only *Artemisia tridentata*, and the geographical area occupied by ssp. *feudgei* coincides rather well with the southwestern range of that *Artemisia* (Ward, 1953).

Some morphological variation is worth noting. The most striking is an atypical corolla that has a narrower sinus of the lower tube and an upper flaring tube with narrower and more pointed lower lobes, all features of ssp. *jepsonii*, rather than the characteristic broad tube of ssp. *feudgei*. These variants, however, have the typical habit of ssp. *feudgei* and are scattered throughout the range of this subspecies (Kern Co.: *Breedlove 3874*; San Diego Co.: *Northrup* in 1935). In addition, the host for one of the collections (*Breedlove 3874*) is noted as *Artemisia tridentata*.

There appears to be some intergradation of ssp. *feudgei* with those subspecies with juxtaposing ranges, i.e., ssp. *grandis* and *condensa*, as discussed under those subspecies. There is no evidence of intergradation with *O. vallicola* of lower elevations.

The most intriguing relationship of ssp. *feudgei* is that to *O. corymbosa* (Rydb.) Ferris, which appears to be a reduced version of ssp. *feudgei* with the same host preference. Collins (1973) has pointed out the usefulness of placentation for *Orobanche* taxonomy and the arrangement of the placenta can be used to distinguish the two taxa: *O. corymbosa* has two parietal placentae per ovary while in ssp. *feudgei* (and all of *O. californica*) each of these two placental areas is separated into two distinct placentae, thus forming four placentae per ovary. This feature shows up well either in the ovary or in the dehisced carpel. Corolla color also seems to be a consistent difference between the two taxa with *feudgei* having a much lighter corolla than *corymbosa*, in which the corolla lips are a deeper purplish or maroon. Where the ranges of the two species approach each other (southern Sierra Nevada, Tulare Co., and Piute Mts., Kern Co.), there is no definite evidence of intergradation. Variant specimens of ssp. *feudgei* are present in the Piute Mts. but are not clearly intermediate between the two species. One specimen (*Twisselmann 7358*, JEPS) has a corolla that is more similar in size and shape to that of other subspecies of *O. californica* in its narrower lip lobes and widely flaring lips. The other specimen (*Smith 864*, JEPS), unfortunately a fasciated

one, has a corolla like that of *corymbosa* but with the habit and size more like *feudgei*.

2. **Orobanche vallicola** (Jepson) Heckard, stat. et comb. nov.

O. comosa var. *vallicola* Jepson, Man. Fl. Pl. Calif. 952. 1925. TYPE: California: Santa Clara Co.: river bottom, Coyote, *Jepson 6196* (HOLOTYPE: JEPS!; ISOTYPE: GH!, MO!).

O. californica var. *claremontensis* Munz, Bull. Torrey Bot. Club 57: 618. 1931. TYPE: California: Los Angeles Co.: Claremont, *D. L. Crawford 574*, 8 Jul 1916. (HOLOTYPE: POM!; ISOTYPES: DS!, UC!).

Plants single-stemmed or sparingly branched at base, 7–40 cm long, the underground stem below the inflorescence 5–30 cm long and up to 20 mm in diameter; scales broad and obtuse on lower stem, narrowing upwards on stem and becoming narrow-triangular to subulate as bracts in the inflorescence; inflorescence subspicate or racemose, occasionally paniculate, 4–30 cm long, glandular-puberulent throughout; lower pedicels 5–25 mm long, usually decreasing in length upwards, bearing opposite subulate bracts 5–10 mm long; calyx lobes narrow-subulate, often with the apex attenuate, (6) 9–15 (20) mm long, pale or pinkish tinged, the tips sometimes revolute; corolla 17–28 (30) mm long, whitish or yellowish to pinkish tinged, often with the veins of lips and upper tube darker pink or purplish, the palatal folds yellow; corolla lips usually widely spreading, 5–9 (10) mm long, the upper corolla lobes triangular or triangular-ovate with acute and pointed apex; lower corolla lobes narrow-triangular to lanceolate with acute apex; anthers ca 1.5 mm long, glabrous or villous in varying degrees along the dehisced margins; stigma bilamellate with strongly downward curving lobes or somewhat peltate-crateriform with margins rolled downward; capsule ovoid to cylindrical-ovoid, 10–13 mm long; seed ovoid, ca 0.5 mm long.

Hosts: Frequently reported to be parasitic on *Sambucus*. Also reported on pear [*Pyrus*] (*Chandler*, Oct 1905), *Quercus agrifolia* (*Crawford 547*), *Symphoricarpos albus* (*Linsdale 259*), *Baccharis douglasii* (*Jepson 6196*).

DISTRIBUTION: Woodlands, thickets, and openings, lowland valleys and foothills; occasional in widely scattered localities, cismontane California from Trinity Co. S to Los Angeles Co. Rare. May–Nov (as early as Mar in S. Calif). Known localities (fig. 5):

CALIFORNIA: TRINITY CO.: Hyampum, *Blasdale*, 11 Jun 1896 (UC). SHASTA CO.: Anderson, *Rich*, Nov 1921 (DS). TEHAMA CO.: S rim of Mill Creek Canyon *Quick 49–47* (CAS). BUTTE CO.: Chico, *E. Copeland*, 2 Nov 1936 (UC). COLUSA CO.: Princeton, *Chandler*, Oct 1905 (UC); Sycamore Slough, *Stinchfield*, 12 Jul 1916 (DS). SACRAMENTO CO.: Sacramento, *Savage*, 11 Jun 1964 (CDA). MENDOCINO CO.: Covelo, *Murphey*, 16 Oct 1946 (OSC). LAKE CO.: Kelsey Creek, ca 2 mi S of Kelseyville, *Schulthess*, 13 July 1931 (UC). SONOMA CO.: Russian River near Cloverdale, *Lile*, 1 Oct 1933 (UC,

JEPS). MARIN CO.: Novato, *Kessel*, 16 Sep 1956 (JEPS); San Anselmo Canyon, *Sutcliffe*, Oct 1924 (CAS). ALAMEDA CO.: Centerville, *Gammon*, Aug 1955 (CDA); near Livermore, *Hammond*, Aug 1896 (JEPS). CONTRA COSTA CO.: Russellmann Park, N base of Mt. Diablo, *R. Smith*, 23 Sep 1956 (JEPS); Marsh Creek road, 3 mi above Clayton, *Mason 5432* (JEPS). SAN JOAQUIN CO.: Mokelumne River, Lodi, *Switzenberg*, 13 Jul 1964 (CDA). STANISLAUS CO.: Tuolumne River bottom, Empire, *E. Morse*, 10 Jun 1939 (JEPS). SANTA CLARA CO.: Mt. Hamilton, *R. Smith 10* (UC); Saratoga, *Fablinger*, Oct 1894 (UC). MONTEREY CO.: Hastings Reservation, Santa Lucia Mts., *Linsdale 259* (CAS); Redwoods, Santa Lucia Mts., *Palmer 338* (F, GH, MO, UC, US). SAN BENITO CO.: Zanger Ranch, Pacheco Pass highway, *Dermody*, 18 Aug 1965 (CDA). SAN LUIS OBISPO CO.: Atascadero, *Huffman*, 11 Nov 1964 (OBI). FRESNO CO.: San Joaquin River bottom, N of Fresno, *Quibell 2084* (RSA). SANTA BARBARA CO.: Figueroa Mt., *Hoffman*, 7 Jun 1929 (SBM). LOS ANGELES CO.: Tick Canyon, *MacFadden 16187* (CAS); Santa Monica Canyon, *Barber*, 3 Jul 1898 (UC); Claremont, *Harwood 3275* (POM).

This species has essentially the same circumscription as the combined concepts of *O. californica* vars. *californica* and *claremontensis* in Munz (1930). Munz's var. *claremontensis*, a local variant from the Claremont region of eastern Los Angeles Co., was distinguished by a deeply cut upper lip of the corolla. I have examined another collection (*Harwood 3275*) from this locality with corollas less deeply cut (about $\frac{1}{2}$ the lip length) than those of the type collection, indicating that this feature is a variable one in this region and does not in itself justify varietal rank for the plants.

A baffling relationship of this species, as well as one that gives difficulty in identification, is that with *O. californica* ssp. *jepsonii*. The separation of these two largely sympatric taxa (fig. 5) is sometimes difficult owing to the variability of their diagnostic features. The two taxa are distinguished by a combination of characters, no one of which is absolute, at least as seen in herbarium materials, and any of the characters can be variable and intergrading between the two species. Thus *vallicola* typically has a stem that is more thickened basally and that becomes darker on drying; the inflorescence is subspicate with only the lowermost flowers having pedicels, in contrast to the racemose or paniculate inflorescence of ssp. *jepsonii* with longer pedicels nearly throughout; similarly the calyx lobes are usually shorter in *vallicola*. The corolla of *vallicola* is typically smaller, the lips shorter with narrower, more pointed lobes; the anthers are slightly smaller than those of ssp. *jepsonii* and are either glabrous or at least less villous, with the hairs largely confined to the region of dehiscence. Perhaps the most consistent feature of *vallicola* is a stigma in which the lobes are decurved apically (fig. 4, J-L) and often laterally, thus becoming crateriform (fig. 4, L) in contrast to the spreading, laminate, and triangular lobes of the stigmas of ssp. *jepsonii*

(fig. 4, F). Data on hand suggest a difference in host preference with *vallicola* usually parasitic on trees or occasionally shrubs, whereas ssp. *jepsonii* is usually reported on *Grindelia* or other herbaceous perennials of the Compositae. The report of the type specimen of *O. californica* ssp. *jepsonii* on the shrub *Baccharis viminea* is an exception.

Recognition of the *vallicola* plants as a species apart from *O. californica* ssp. *jepsonii* follows previous workers (Beck, 1930; Munz, 1931; Ferris, 1960), who also recognized and commented on the close affinity of the two. In spite of the overlap in diagnostic features separating these two largely sympatric groups, two recognizable forms emerge that seem adequately distinct for recognition as separate species.

3. *Orobanche parishii* (Jepson) Heckard, comb. et stat. nov.

Orobanche californica var. *parishii* Jepson, Man. Fl. Pl. Calif. 952. 1925. TYPE: California: San Bernardino Co.: Bear Valley, San Bernardino Mts., S. B. Parish in 1894 (HOLOTYPE: JEPS!).

Plants single-stemmed or sparingly branched at base, the stems 5–26 cm in length and up to 15 mm in diameter, simple or occasionally branched above; scales broadly ovate becoming (as bracts) lance-ovate or broadly triangular in the inflorescence, multi-veined with more than 5 conspicuous parallel veins; inflorescence subspicate, usually densely glandular-puberulent throughout, the flowers mostly sessile with the lowermost occasionally on short pedicels rarely over 1–2 cm long; bractlets opposite, subulate, less than 10 mm long; calyx lobes subulate to subulate-attenuate, 6–18 mm long, pallid or pinkish to purplish tinged; corolla 15–25 mm long, curving outward in older flowers, whitish or yellowish to buff, the lips buff to pinkish with maroon veins or tinged with purplish-red, moderately to sparsely glandular externally; corolla lips 4–8 mm long, erect to spreading or recurved, the upper lip cleft 2–3 mm into 2 oblong or oblong-ovate lobes with rounded to truncate and often retuse or erosulate apices; lower lobes of corolla narrower, rounded or blunt at tip, often retuse or erosulate; palatal folds of the tube well developed; anthers 1.5–2.0 mm long, glabrous or moderately villous along the dehisced margins; stigma bilobed, often unequally so, the triangular or rounded lobes thin or thick, spreading to recurving; capsule oblong-ovoid, 7–10 mm long; seed brown, irregularly ovoid, favose-reticulate, ca 0.4–0.5 mm long.

HOST: Various shrubs and herbaceous perennials; apparently different for the two subspecies, q.v.

DISTRIBUTION: Southern California and northern Baja California. Rare (fig. 5).

In elevation of *O. californica* var. *parishii* to a species, the prevailing concept of the group as one of montane Southern California is expanded not only to include plants of the surrounding lowland areas but also to add a new subspecies to accommodate related plants of the California Channel Islands and coastal mainland.

The plants are rare and information on habitat and hosts, flower color, and chromosome number is scanty. Only two chromosome counts are available (Chuang & Heckard, in prep.), a count of $n = 24$ for ssp. *parishii* and one of $n = 48$ for ssp. *brachyloba*.

KEY TO SUBSPECIES OF *O. PARISHII*

- Corolla 2.0–2.5 cm long with corolla lips 6–8 mm long; calyx lobes subulate-attenuate, mostly 10 mm or longer; anthers hairy or occasionally glabrous; stigma lobes thin, spreading but not recurving; mostly montane, Southern California ssp. *parishii*
- Corolla 1.5–2.0 cm long with lips 4–6 mm long; calyx lobes subulate, usually less than 10 mm long; anthers glabrous; stigma lobes thick and usually recurving outwardly; California Channel Islands, rare on coastal mainland ssp. *brachyloba*

3a. OROBANCHE PARISHII (Jeps.) Heckard ssp. PARISHII

Stem simple, 15–22 (10–26) cm long; inflorescence 5–8 (3–14) cm long and 2.5–4.0 cm broad, narrow and moderately dense; calyx-lobes 10–13 (6–18) mm long, the tips often recurving; corolla 18–25 mm long, often sharply curved at nearly a right angle to the axis in older flowers, yellowish or lavender-tinged with darker veins, in dried specimens the lips brownish or buff with 3 conspicuous maroon veins; upper lips spreading or recurved, lower lips spreading; anthers moderately villous along the dehisced margins, occasionally glabrous; stigma bilobed, often unequally so, funnellform, the lobes thin, spreading

HOST: Reported to be mostly parasitic on shrubs: *Adenostoma* (Percison 416), *Arctostaphylos* (Fosberg, 12 Aug 1931), *Eriodictyon* (Johnston 1762). Also reported on *Corethrogyne filaginifolia* (Wallace 562).

DISTRIBUTION: Open chaparral or scrub, 600–2,100 m (rarely 150–2,700 m) elevation. Mountains of cismontane Southern California: Kern Plateau, Tulare Co., and Mt. Pinos, Ventura Co., S to the Sierra San Pedro Martir of Baja California. Rare in the Mohave Desert. Mar–Sep (Nov). Known localities (fig. 5):

CALIFORNIA: TULARE CO.: Kennedy Meadows, Kern Plateau, Howell & True 43822 (CAS); N end of Lamont Meadow, Howell & True 43758 (CAS). VENTURA CO.: Iris Point, Mt. Pinos, Heckard & Chuang 2732 (JEPS); Topatopa Mts., Red Reef Canyon, Abrams & McGregor 127 (DS). KERN CO.: Old Fort Tejon, Tehachapi Mts., Hall 6301 (UC), Coville & Funston 1159 (US) [both specimens aff. *O. vallicola*—see text]. SAN BERNARDINO CO.: Mohave Desert, Victor, Wright, June 1888 (UC); Old Dad Mt., Cottonwood Spring, M. Jones, 14 May 1926 (POM); San Bernardino Mts., above Lake Arrowhead, Clokey 5308 (UC); San Antonio Mts., Devils Backbone, Johnston 1762 (UC). LOS ANGELES CO.: San Gabriel Mts., Mt. Islip summit, Fosberg & Ewan 792 (LAM); San Gabriel Mts., Arraster Creek, Pierson 416 (JEPS); N of River Reservoir, Davidson, Aug 1889

(LAM); Santa Anita Canyon, *Moxley*, 1 Sep 1913 (LAM). RIVERSIDE CO: San Jacinto Mt., *Hoffman*, 8 Sep 1929 (SBM); Joshua Tree National Monument, Smith Water Canyon, *Schenk* (RSA); Box Springs Mt., near Riverside, *Wallace 562* (POM). SAN DIEGO CO.: Warner Hot Spring Mt., Eagle Nest, *Gander 286* (SD); Julian, *T. Brandegee*, 12 Jun 1894 (UC); Ramona, *T. Brandegee*, 29 May 1894 (UC).

BAJA CALIFORNIA: La Encantada, Sierra San Pedro Martir, *Wiggins 16623* (DS).

Removal of plants of ssp. *parishii* from their taxonomic alignment as a variety of *O. californica* (= *O. vallicola* in this treatment) is based on the consistent differences in corolla and bract between the two groups and on their sympatric association in the Los Angeles basin without their loss of identity. The bract (fig. 3, L-N) is broader than in *O. vallicola* and has a larger number (over five) of parallel veins and the corolla has broader lobes that are obtuse and rounded at the apex rather than acute and pointed. There are also differences in corolla color and texture in the dried specimens, the corolla of ssp. *parishii* being buff-colored (off-white to yellowish in *O. vallicola*) often with reddish-brown lobes and veins (purplish in *O. vallicola*). In texture the corolla of ssp. *parishii* is thicker and less brittle. It seems likely that these corolla features will be even more pronounced in fresh material.

Two specimens that appear to be intermediate between ssp. *parishii* and *O. vallicola* have been collected near Fort Tejon in Kern Co. The earlier collection (*Coville & Funston 1159*) in 1891 shows a greater resemblance to *O. vallicola* than does the collection of 1905 (*Hall 6301*). This later collection, however, possesses the long, narrow, pointed lower lobes of the corolla that is typical of *O. vallicola*.

3b. *Orobanche parishii* ssp. *brachyloba* Heckard, ssp. nov.

TYPE: CALIFORNIA: Ventura Co.: Dutch Harbor, San Nicolas Island, *Raven & Thompson 20794* (HOLOTYPE: JEPS; ISOTYPES: DS, RSA).

Plantae 5–18 cm altae; inflorescentia subspicata, crebra, 3–10 (15) cm longa; calycis lobi 7–9 (11) mm longi; corolla 15–24 mm longa, demum sursum vel horizontaliter curvata, plerumque glandulosissima, fulva, plerumque violaceotincta; corollae labia 4–7 mm longa, antherae glabrae (raro glabrescentes); stigma bilobata, lobis eius crassis decurvatis.

Plants with 1 stem or several from branching base; stem simple or occasionally with a few secondary branches from the midpoint or below, 5–18 cm long; inflorescence subspicate, dense, 3–10 (15) cm long; calyx lobes 7–9 (11) mm long, subulate; corollas 15–24 mm long, directed upwards or curving outward in age, usually abundantly glandular, buff to yellowish, often tinged along veins of lips with purplish-red; corolla lips 4–7 mm long, erect or slightly spreading; anthers glabrous (rarely sparsely villous); stigma bilobed, the lobes usually thick and

strongly decurving, sometimes crateriform.

HOST: Mostly reported to be growing on *Haplopappus* (usually *H. venetus*); *Atriplex californica* (*Philbrick B65-1526*) and *Eriogonum latifolium* (*Benedict, 10 Sep 1967*) also are suspected hosts.

DISTRIBUTION: Sandy soil near beaches. Santa Barbara Channel Islands and San Nicolas and Santa Catalina islands of California; occasionally on the mainland in San Luis Obispo and San Diego counties and in Baja California. May–Sep. Known localities (fig. 5):

CALIFORNIA: SAN LUIS OBISPO CO.: dunes S of Oso Flaco Lake, *Hoover 10870* (OBI). **SANTA BARBARA CO.:** San Miguel Island: Cuyler Harbor, *Blakley 5875* (JEPS), Harris Point peninsula, *Philbrick B65-1526* (SBBG); Santa Rosa Island: W end, *Hoffman, 9 Aug 1930* (CAS, SBM); Santa Cruz Island: S end of Christi Beach, *Benedict, 10 Sep 1967* (SBBG). **VENTURA CO.:** San Nicolas Island: Jackson Hill road to beach (W side), 700 ft, *Blakley 4157* (SBBG). **LOS ANGELES CO.:** Santa Catalina Island: Ben Weston Beach, *Thorne & Everett 34392* (JEPS, RSA, SBBG). **SAN DIEGO CO.:** Silver Strand, *Purer 2923* (SD).

BAJA CALIFORNIA: El Rosario, *T. Brandegee, 20 May 1889* (F).

Plants of this largely insular subspecies differ from those of ssp. *parishii*, a mainland and largely montane group, in several minor features that in their total effect present two easily recognizable entities. Variation of these features within each subspecies, however, results in an overlap in these definitive characters that makes it difficult to formulate a key that allows decisive identification in all cases. These differences consist of an overall decrease in size in ssp. *brachyloba*: the stems and inflorescence are shorter, the corolla and calyx-lobes are shorter. In addition, ssp. *brachyloba* has shorter corolla lips that are erect or only slightly spreading rather than recurved and their color, at least in pressed specimens, is a purplish-red tinge throughout while ssp. *parishii* has buff or yellowish lips with conspicuous maroon veins. The corollas of ssp. *brachyloba* are not as conspicuously curved outward in older flowers as in ssp. *parishii*. Glabrous anthers and a very dense spike are the usual condition for *brachyloba*, whereas the anthers of ssp. *parishii* are more often hairy and the flowers of the spike are less crowded. Although sporadic variation may occur in any of these features, the overall difference between the two groups warrants their taxonomic recognition. One variant deserves special mention: The only collection from Santa Catalina Island (*Thorne & Everett 34392*) approaches ssp. *parishii* in almost all the above features. Because of its similarity in habitat and geography with ssp. *brachyloba*, however, I am assigning this collection to that taxon.

There are some differences among the collections from different islands, probably reflecting the independent evolution of the isolated populations. Plants from San Nicolas Island (*Raven & Thompson 20794*) in general possess the most distinctive features in comparison

to ssp. *parishii*. Plants from the northern islands along the Santa Barbara Channel are fairly similar but have more pointed corolla lobes.

Three collections from the coastal mainland seem more similar to the island plants than to the montane plants of ssp. *parishii*. One, a collection from San Luis Obispo Co. (*Hoover 10870*), is unusual in having anthers that are sparsely hairy and lower corolla lobes that are broader than usual.

The only other species of the *O. californica* complex that has been collected from the Channel Islands is *O. californica* ssp. *grandis*, on Santa Rosa Island (*Hoffman, SBM*).

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